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# Relation Between $S_2$ and Later Generation Testcrosses of Two Corn Populations[1]

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Determination of the relative combining abilities of corn (*Zea mays* L.) inbred lines is an important feature of applied corn breeding programs. Combining ability is measured by the relative performance of a line in testcrosses to one or more testers. Inbred lines from BS13(S2)C1 and BSCB1(R)C7 corn populations were evaluated at the $S_2$ and later generations of inbreeding. Intense selection was practiced among and within lines during inbreeding to develop the $S_5$-equivalent and $S_8$ generation lines. The objective of this study was to determine if the combining ability of lines in early generations ($S_2$) of inbreeding was similar to the combining ability of lines at later generations of inbreeding. Testcross trials were conducted at four Iowa locations. Genetic correlations between the $S_2$ and later generation testcrosses for grain yield were 0.97 for BS13(S)C1 and 0.86 for BSCB1(R)C7. The $S_2$ testcross data were highly predictive of $S_8$ testcross data, suggesting that early testing was effective in discriminating among these lines for relative combining abilities at later generations of inbreeding.

INDEX DESCRIPTORS: *Zea mays* L.; corn breeding; combining ability; inbred lines

Corn (*Zea mays* L.) breeding methods described by Shull (1909) included development of pure lines (inbred lines) and determining the best hybrid among crosses of the inbred lines. Pedigree selection methods are used to develop inbred lines with selection among and within lines at all levels of inbreeding. This process is continued until the desired level of homozygosity (usually $S_5$ to $S_7$ generations of selfing) has been attained. Selection among and within lines during inbreeding can emphasize pest resistance, maturity, plant type, root and stalk strength, and performance in crosses. Because of the relatively higher heritability of some traits (e.g., maturity) and the development of artificial methods of infection for diseases and infestation for insects, selection among and within progenies is usually effective for these traits in the breeding and pest nurseries.

Determination of the performance of lines in crosses (i.e., combining ability) requires greater resources because crosses are evaluated in replicated trials conducted in different environments. The initial evaluations usually include crossing all lines to a common tester(s) to determine the relative combining ability of the new lines. Lines having above average combining ability are continued for further selection in breeding nurseries and further evaluation in crosses with other elite lines to identify superior hybrids. The level of inbreeding considered for the initial evaluation of new lines differs among corn breeders. Bauman (1981) reported that 18% of corn breeders tested new lines at $S_2$ generation, 33% at $S_3$ generation, 27% at $S_4$ generation, and 22% at $S_5$ or later generations. Proponents of early generation testing (e.g., $S_0$ to $S_2$ generations) suggest that the relative combining abilities of lines were relatively stable from the $S_1$ generation through subsequent selfed generations (Jenkins, 1935; Sprague, 1946). Proponents of later-generation testing (e.g., $S_4$ to $S_7$ generations) suggest that the combining abilities of lines at the $S_1$ generation are not good predictors of combining abilities at later generations of inbreeding and that evaluation of lines be delayed after further inbreeding and selection (Richey, 1945; Singleton and Nelson, 1945; Payne and Hayes, 1949). Supporters of early testing do not claim that an exact ranking of lines will occur at two different stages of inbreeding, but that further inbreeding and selection should emphasize only lines having above-average combining ability.

The objectives of our study were to evaluate the effects of intense selection for agronomic traits among and within progenies during inbreeding by comparison of means and variances $S_2$ and later generation testcrosses and to determine the genetic associations between $S_2$ and later generation testcrosses. Two sets of lines were evaluated as $S_2$ and as $S_5$-equivalent and $S_8$ generation testcrosses.

## MATERIALS AND METHODS

The genetic materials evaluated were derived from the BS13 (S2)C1 and BSCB1 (R)C7 populations. The BS13(S2)C1 population was developed from Iowa Stiff Stalk Synthetic (BSSS) by seven cycles of half-sib recurrent selection and one cycle of $S_2$ recurrent selection (Smith, 1983). BSCB1(R)C7 population was developed from Iowa Corn Borer Synthetic No. 1 (BSCB1) by seven cycles of reciprocal half-sib recurrent selection with BSSS(R) as the tester (Smith, 1983).

Unselected $S_0$ plants were self-pollinated within BS13(S2)C1 and BSCB1(R)C7 to produce $S_1$ seed in 1975. Two systems of inbreeding (self and full-sib) were used to develop two groups of lines within BS13(S)C1 and BSCB1(R)C7 in the $S_1$ generation. Seed of $S_1$ lines was planted on an ear-to-row basis, and seed was produced within each $S_1$ row by self-pollination and full-sib pollination. No selection was applied at the $S_1$ generation. Within the self-pollinated group of lines, seed of each generation of self-pollination was planted ear-to-row, and selection among and within progeny rows was practiced for seven generations until the lines were nearly homozygous (F=0.996). Within the full-sib group of $S_1$ lines, full-sib pollinations of selected plants within each progeny were continued for four generations, followed by two generations of self-pollination (F=0.969); selections were made within and among progeny rows for each generation of sib-mating and selfing. Full-sib mating is a milder form of inbreeding, but the empirical evidence suggests no significant differences between lines developed by selfing and full-sib matings developed from the same genetic source at comparable levels on inbreeding (Kinman, 1952; Cornelius and Dudley, 1974; Good and Hallauer, 1977; Hallauer and Lopez-Perez, 1979). All lines were included in one group for statistical analyses, but the full-sib mated lines were on average less inbred than the self-pollinated lines, or equivalent to $S_5$ generation lines in selfing (Table 1).

Traits considered in selection during inbreeding included resistance to first-generation European corn borer (*Ostrinia nubilalis* Hübner) after application of egg masses; resistance to root and stalk lodging; level of stalk-rot infection after artificial inoculation [*Dipolida zea* Schw., *Gibberella zea* (Schw.) Petch., and *Fusarium moniliforme* Sheld.] and slicing of stalks between second and third internodes; simultaneous silk emergence and pollen shed; ear size and seed set with ears free of diseases; good pollen shed; truncation selection for earlier flowering with discard of later progenies; and

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Table 1. Number of lines retained after selection from BS13(S)C1 and BSCB1(R)C7 populations for each generation on inbreeding.

| Generation | Inbreeding (F) Self | Inbreeding (F) Full-sib | Populations BS13(S2)C1 Self | BS13(S2)C1 Sib | BSCB1(R)C7 Self | BSCB1(R)C7 Sib |
|---|---|---|---|---|---|---|
| | -----%----- | | | | -------no.----- | |
| $S_0$ | 0.0 | 0.0 | 160 | --- | 167 | --- |
| $S_1$ | 50.0 | 50.0 | 160 | 160 | 167 | 167 |
| $S_2$ | 75.0 | 50.0 | 151 | 150 | 156 | 143 |
| $S_3$ | 87.5 | 62.5 | 151 | 92 | 155 | 107 |
| $S_4$ | 93.8 | 68.8 | 93 | 30 | 94 | 51 |
| $S_5$ | 96.9 | 75.0 | 65 | 15 | 51 | 39 |
| $S_6$ | 98.4 | 87.5 | 47 | 10 | 40 | 26 |
| $S_7$ | 99.2 | 93.8 | 46 | 10 | 35 | 24 |
| $S_8$ | 99.6 | 96.9[a] | 46 | 6 | 35 | 16 |
| Total number of lines | | | 52 | | 51 | |

[a]Equivalent to $S_5$-generation for expected level of inbreeding.

general plant health, vigor, and appearance. The numbers of lines retained from each population for each generation of inbreeding are included in Table 1.

Final selections were made among lines after seven generations of inbreeding, and the eighth-generation seed was used for making the testcrosses. After final selections, pedigrees of the selected lines were traced back to the $S_2$ generation seed. The $S_2$ generation lines, therefore, were chosen on the basis of the surviving $S_7$ generation lines. The $S_2$ and later generation testcrosses were made in 1984 and 1985. (Mo17xMBS2040) was the tester for the BS13(S2)C7 lines, and (B73xB84) was the tester for the BSCB1(R)C7 lines. The genetic materials included 52 $S_2$ and later generation testcrosses of BS13(S2)C1 and 51 $S_2$ and later generation testcrosses of BSCB1 (R)C7 (Table 1).

The $S_2$ and $S_8$ testcrosses were evaluated at four Iowa environments (Ankeny, Martinsburg, and two locations near Ames) in 1986. The experimental design employed was a 10 x 11 simple rectangular lattice at each environment for each population. The lattice design for the BS13(S2)C1 population included 104 testcrosses and six checks, whereas the lattice design for the BSCB1(R)C7 population included 102 testcrosses and eight checks. Except to account for the total sum of squares in the analysis of variance, the checks will not be considered in the discussion of the results. Trials were machine-planted in two-row plots, 5.49 m long spaced 76.2 cm between rows. Plots were overplanted and thinned at the four- to six-leaf stage to an equivalent stand of 62,140 plants $ha^{-1}$. Conventional fertilization, weed control, and cultivation practices were used at all environments for high corn productivity. Plots were machine-harvested at all environments.

Data were taken for eight traits for the testcrosses. A severe windstorm 29 July 1986 near Ames and Ankeny caused substantial root and stalk lodging, and data for root and stalk lodging, dropped ears, and ear height were unreliable for these two environments and were omitted from our analysis. Data were taken for grain yield (q $ha^{-1}$), grain moisture at harvest (%), and plant stand (plants $ha^{-1}$) at four environments. Root and stalk lodging (%) and dropped ear (%) data were taken at two environments, whereas number of days from planting to anthesis and ear height (cm) measurements were obtained in one environment.

The original analysis of variance was for a 10 x 11 simple rectangular lattice design. Use of the simple rectangular lattice design showed less than 1% gain in experimental precision compared with the randomized complete-block design for all but one environment. Thus, all statistical analyses were based on a randomized complete-block design for each environment and combined across the four environments. Entry sum of squares was partitioned among $S_2$ and later generation testcrosses, among checks, and mean comparisons of $S_2$ vs. later generation testcrosses, and testcrosses ($S_2$ + $S_8$ ) vs. checks. Environments and replications were considered random effects and entries as fixed effects in deriving expected mean squares. Direct F-tests were available for all sources of variation in the analyses of variance.

On the basis of the expected mean squares, estimates were obtained of the variation among $S_2$ and later generation testcrosses ($\sigma^2_g$), interactions of $S_2$ and later generation testcrosses with environments ($\sigma^2_{ge}$), and experimental errors ($\sigma^2_g$). Estimates of the degree of genetic determination (broad-sense heritability) were calculated for each trait among $S_2$ and later generation testcrosses for each population. Heritability ($h^2$) was calculated on a progeny-mean basis as

$$h^2 = \sigma^2_g/(\sigma^2/re + \sigma^2_{ge}/e + \sigma^2_g),$$

where r is number of replications (r = 2) and e is the number of environments in which data were obtained (e = 2 to 4). Heritability estimates for days from planting to anthesis and ear height were calculated as

$$h^2 = \sigma^2_g(\sigma^2/r + \sigma^2_g),$$

Product-moment phenotypic and genotypic correlations were calculated for each trait between $S_2$ and later generation testcrosses for each population. Phenotypic and genotypic variances and covariances were used to estimate the respective correlations. Spearman's (Snedecor, 1956) rank correlation coefficients were calculated for each trait to measure the relation of ranked data between the $S_2$ and later generation testcrosses for each population. The rank correlation coefficient is an adaptation of the Pearson product-moment coefficient and has the same interpretive values (i.e., −1 to +1).

The $S_5$-equivalent and $S_8$ lines used to produce the $S_5$-equivalent and $S_8$ testcrosses were selected lines, whereas $S_2$ lines used produce the $S_2$ testcrosses had limited selection. Neither the $S_2$ nor the later generation lines had any selection based on testcrosses. Although the lines per se were a selected sample, the testcrosses were considered an unselected sample. Hence, a model II analysis was assumed for estimation of components of variance and covariance.

## RESULTS AND DISCUSSION

Means of the $S_2$ and later generation testcrosses were similar for all traits for both populations (Table 2). The difference between the means of the $S_2$ vs. later generation testcrosses for days to anthesis was highly significant ($P \leq 0.01$) for BS13(S2)C1, but the difference was only 0.4 d; all other $S_2$ vs. later generation testcross mean comparisons for BS13(S2)C1 and BSCB1(R)C7 were not significantly different. Differences among $S_2$ and later generation testcrosses of BS13(S2)C1 were highly significant for all traits except stalk lodging ($P \leq 0.05$) and nonsignificant for root lodging of $S_2$testcrosses and percentage of dropped ears for $S_2$ and later generation testcrosses (analyses not shown). For the BSCB1(R)C7 $S_2$ and later generation testcrosses, differences among testcrosses were highly significant for all traits except percentages of stalk lodging and dropped ears, which were nonsignificant. Interactions of testcrosses by environments for grain yield were significant for $S_2$ testcrosses for BS13(S)C1 and highly significant for later generation testcrosses for BS13(S2)C1 and BSCB1(R)C7. Only two other testcrosses-by-environment interactions were significant [root lodging for BS13(S2)C1 $S_2$ testcrosses and grain moisture for BSCB1(R)C7 $S_8$ testcrosses]. Selection during inbreeding in the development of the $S_5$-equivalent and $S_8$ lines emphasized those traits that were

Table 2. Means (X) ± standard errors and ranges for eight traits of $S_2$ and later generation testcrosses of the BS13(S2)C1 and BSCB1(R)C7 corn populations.

| Trait | Populations | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | BS13(S2)C1 | | | | BSCB1(R)C7 | | | |
| | Mean | | Range | | Mean | | Range | |
| | $S_2$ | $S_8$ | $S_2$ | $S_8$ | $S_2$ | $S_8$ | $S_2$ | $S_8$ |
| Grain yield[a], q $ha^{-1}$ | 78.6 ± 0.4 | 80.2 ± 0.4 | 25.3 | 42.4 | 78.6 ± 0.4 | 79.7 ± 0.5 | 26.9 | 26.4 |
| Grain moisture[a], % | 22.6 ± 0.1 | 22.5 ± 0.1 | 4.0 | 5.0 | 21.3 ± 0.1 | 21.3 ± 0.1 | 3.7 | 4.2 |
| Stand[a], ha $1000^{-1}$ | 59.4 ± 0.1 | 59.2 ± 0.1 | 5.8 | 6.6 | 60.1 ± 0.1 | 59.6 ± 0.2 | 5.9 | 10.5 |
| Root lodging[b], % | 17.6 ± 0.7 | 15.7 ± 0.6 | 30.2 | 36.2 | 16.5 ± 0.7 | 18.2 ± 0.7 | 31.7 | 48.2 |
| Stalk lodging[b],% | 4.8 ± 0.2 | 4.6 ± 0.3 | 17.7 | 11.1 | 5.6 ± 0.2 | 5.3 ± 0.3 | 9.9 | 11.7 |
| Dropped ears[b], % | 0.9 ± 0.1 | 0.9 ± 0.1 | 5.1 | 4.1 | 0.3 ± 0.1 | 0.3 ± 0.1 | 2.0 | 1.5 |
| Days to anthesis[c], no. | 82.8 ± 0.1 | 82.4 ± 0.1 | 6.0 | 5.5 | 83.0 ± 0.1 | 82.9 ± 0.1 | 5.5 | 6.0 |
| Ear height[c], cm | 124.5 ± 0.6 | 124.2 ± 0.6 | 38.2 | 44.3 | 125.6 ± 0.5 | 126.6 ± 0.5 | 45.6 | 37.4 |

[a]Means for four environments.
[b]Means for two environments.
[c]Means for one environment.

considered important for lines to be used as parents of hybrids. Selection among lines per se did not affect the mean performance of the $S_2$ and later generation testcrosses (Table 2). Selection among and within lines during inbreeding also did not affect the variability among $S_2$ and later generation testcrosses because levels of significant differences among testcrosses were similar (analyses not shown). There were no consistent trends for the magnitude of the $S_2$ and later generation testcross mean squares for the eight traits, but the late generation testcross mean squares were 30% greater than $S_2$ testcross mean squares for grain yield and moisture for both populations. Neither of these traits, however, was considered in the selection of the lines themselves. Greater variation among later generation testcrosses compared with among $S_2$ testcrosses may have been because of the greater inbreeding level of $S_8$ lines.

Estimates of the genotypic components of variance for $S_2$ and later generation testcrosses ($\sigma^2_g$), their interactions with environments ($\sigma^2_{ge}$), experimental errors, and heritabilities ($h^2$) were similar for both sets of testcrosses for both populations (Table 3). For grain yield, for example, the estimate of $\sigma^2_g$ for later generation testcrosses was greater than for $S_2$ testcrosses for BS13(S2)C1, but the estimates of ($\sigma^2_g$) for $S_2$ and later generation testcrosses were the same for BSCB1(R)C7. The estimates of $\sigma^2_{ge}$ for grain yield were greater for later generation testcrosses, being significantly greater for BSCB1(R)C7. Heritability estimates for grain yield were similar for both the $S_2$ and later generation testcrosses for both populations, and the $h^2$ estimates are similar to other estimates obtained for testcrosses with inbred testers (Lamkey and Hallauer, 1987). Estimates of components of variance and heritabilities were similar for $S_2$ and later generation testcrosses for both populations except for a few instances (e.g., root lodging for both populations). Heritability estimates were consistently greater than 0.7 for grain moisture, days to anthesis, and ear height; intermediate for grain yield and root lodging; and generally less than 0.4 for stalk lodging and dropped ears (Table 3).

Phenotypic ($r_p$) and genotypic ($r_g$) correlations were calculated between traits for the $S_2$ and later generation testcrosses of both populations, but only 11 of 84 possible phenotypic correlations were significant (correlations are not included). Only one $r_p$ (grain

Table 3. Estimates of genotypic ($\sigma^2_g$), genotype by environment interaction ($\sigma^2_{ge}$), experimental error ($p^2$), and broad-sense heritability ($h^2$) for $S_2$ and later generation testcrosses of the BS13(S2)C1 and BSCB1(R)C7 corn populations.

| Trait | | BS13(S2)C1 | | | | BSCB1(R)C7 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | $\sigma^2_g$ | $\sigma^2_{ge}$ | $\sigma^2$ | $h^2$ | $\sigma^2_g$ | $\sigma^2_{ge}$ | $\sigma^2_g$ | $h^2$ |
| Grain yield | $S_2$ | 13.0 ± 6.0 | 15.5 ± 8.2 | 99.7 ± 6.7 | 0.44 ± 0.28 | 17.1 ± 6.7 | 2.0 ± 8.3 | 121.0 ± 8.2 | 0.52 ± 0.20 |
| (q $ha^{-1}$) | $S_8$ | 23.2 ± 12.1 | 21.5 ± 8.8 | 99.7 ± 6.7 | 0.38 ± 0.20 | 18.3 ± 9.1 | 42.0 ± 12.5 | 121.0 ± 8.2 | 0.42 ± 0.21 |
| Grain moisture | $S_2$ | 0.6 ± 0.2 | −0.1 ± 0.1 | 2.2 ± 0.1 | 0.72 ± 0.19 | 0.6 ± 0.2 | −0.1 ± 0.1 | 1.8 ± 0.1 | 0.76 ± 0.20 |
| (%) | $S_8$ | 0.9 ± 0.2 | 0.2 ± 0.2 | 2.2 ± 0.1 | 0.73 ± 0.20 | 0.7 ± 0.2 | 0.4 ± 0.2 | 1.8 ± 0.1 | 0.69 ± 0.20 |
| Root lodging | $S_2$ | 25.6 ± 18.3 | 35.2 ± 21.5 | 140.2 ± 13.4 | 0.33 ± 0.23 | 32.0 ± 17.7 | 8.7 ± 19.6 | 165.8 ± 15.9 | 0.40 ± 0.23 |
| (%) | $S_8$ | 38.5 ± 15.0 | −6.8 ± 14.0 | 140.2 ± 13.4 | 0.55 ± 0.21 | 61.2 ± 25.1 | 26.3 ± 22.8 | 165.8 ± 15.9 | 0.53 ± 0.22 |
| Stalk lodging | $S_2$ | 3.4 ± 0.2 | −1.4 ± 2.4 | 24.1 ± 2.3 | 0.39 ± 0.23 | 1.1 ± 2.0 | −0.9 ± 2.9 | 27.8 ± 2.7 | 0.14 ± 0.26 |
| (%) | $S_8$ | 2.9 ± 0.2 | −2.2 ± 2.2 | 24.1 ± 2.3 | 0.37 ± 0.23 | 0.8 ± 2.2 | 1.3 ± 3.2 | 27.8 ± 2.7 | 0.10 ± 0.26 |
| Dropped ears | $S_2$ | −0.1 ± 0.3 | 0.5 ± 0.4 | 3.0 ± 0.3 | ----[a] | 0.1 ± 0.1 | −0.1 ± 0.1 | 1.1 ± 0.1 | 0.22 ± 0.26 |
| (%) | $S_8$ | 0.1 ± 0.2 | −0.1 ± 0.3 | 3.0 ± 0.3 | 0.10 ± 0.26 | 0.1 ± 0.1 | −0.2 ± 0.1 | 1.1 ± 0.1 | 0.36 ± 0.23 |
| Days to anthesis | $S_2$ | 1.7 ± 0.4 | ----[b] | 0.9 ± 0.1 | 0.79 ± 0.20 | 1.4 ± 0.3 | ----[b] | 0.7 ± 0.1 | 0.81 ± 0.20 |
| (no.) | $S_8$ | 2.0 ± 0.5 | ----[b] | 0.9 ± 0.1 | 0.82 ± 0.20 | 1.8 ± 0.4 | ----[b] | 0.7 ± 0.1 | 0.84 ± 0.20 |
| Ear height | $S_2$ | 56.9 ± 14.1 | ----[b] | 37.6 ± 5.0 | 0.65 ± 0.20 | 34.6 ± 10.7 | ----[b] | 28.4 ± 3.8 | 0.80 ± 0.20 |
| (cm) | $S_8$ | 64.3 ± 15.5 | ----[b] | 37.6 ± 5.0 | 0.78 ± 0.20 | 67.6 ± 17.0 | ----[b] | 28.4 ± 3.8 | 0.82 ± 0.20 |

[a]Estimate of $h^2$ not available because of negative estimate of $\sigma^2_g$
[b]Data collected in one environment.

yield and root lodging) was consistent for the two populations for the $S_2$ testcrosses. The genetic correlations tended to be larger than the phenotypic correlations, but they were not consistent either between the $S_2$ and later generation testcrosses or between the two populations.

The correlations between the $S_2$ and later generation testcrosses for the same traits were of greater interest (Table 4). The phenotypic correlations were highly significant for all traits except percentage of stalk lodging and percentage of dropped ears for both populations. Genetic correlations were greater than the phenotypic correlations, except for percentage of dropped ears for BSCB1(R)C7. The greatest difference between the phenotypic ($r_p$ = –0.12) and genotypic ($r_g$ + –0.96) correlations was for percentage of stalk lodging for BS13(S2)C1. The genetic correlations ranged from $r_g$ = 0.61 (percentage of root lodging) to $r_g$ = 0.97 (grain yield) for BS13(S2)C1 and from $r_g$ = 0.59 (ear height) to $r_g$ = 0.91 (grain moisture) for BSCB1(R)C7. The genetic correlations of later generation testcross grain yields with $S_2$ testcross grain yields, were $r_g$ = 0.97 for BS13(S2)C1 and rg = 0.86 for BSCB1(R)C7. The coefficients of determination ($r_2$) are 94.1% for BS13(S2)C1 and 74.0% for BSCB1(R)C7, indicating that a large proportion of the genetic variation among the later generation testcrosses was explained by the genetic variation among the $S_2$ testcrosses. $S_2$ testcross performance, therefore, was a good predictor of later generation testcross performance. Spearman's rank correlations ($r_s$) were similar to the phenotypic correlations for all traits (Table 4).

**Table 4. Phenotypic ($r_p$), genetic ($r_g$), and Spearman's rank correlations ($r_s$) between traits of $S_2$ and later generation testcrosses of the BS13(S2)C1 and BSCB1(R)C7 corn populations.**

| | Populations | | | | | |
|---|---|---|---|---|---|---|
| | BS13(S2)C1 | | | BSCB1(R)C7 | | |
| Trait | $r_p$ | $r_g$ | $r_s$ | $r_p$ | $r_g$ | $r_s$ |
| Grain yield | 0.59** | 0.97 | 0.46** | 0.49** | 0.86 | 0.50** |
| Grain moisture | 0.47** | 0.66 | 0.40** | 0.65** | 0.91 | 0.65** |
| Root lodging | 0.43** | 0.61 | 0.39** | 0.45** | 0.69 | 0.56** |
| Stalk lodging | –0.12 | –0.96 | 0.21 | 0.10 | 0.37 | –0.11 |
| Dropped ears | 0.00 | –0.22 | 0.14 | 0.08 | ----[a] | –0.02 |
| Days to anthesis | 0.74** | 0.83 | 0.53** | 0.52** | 0.64 | 0.76** |
| Ear height | 0.60** | 0.78 | 0.56** | 0.51** | 0.59 | 0.58** |

**Significant at the 0.01 probability level.
[a]Negative estimates of genotypic variance among $S_2$ and $S_8$ testcrosses.

Selection at each generation of inbreeding for the development of the $S_5$-equivalent and $S_8$ lines was designed to mimic the selection in applied breeding programs; i.e., healthy plants with strong roots and stalks, good seed set with ears free of diseases, good pollen production, simultaneous silk emergence and pollen shed, and proper maturity. Plants were discarded that exhibited susceptibility to first- and second-generation European corn borer infestation and exhibited diseases in the roots and stalks. Selection pressure for the different traits differed among generations of inbreeding, dependent on environmental conditions that affected the expression of traits during the selfing generations (or years). No information on combining ability was available during the course of selection. Selection was based only on the traits of the inbred lines themselves.

Jenkins (1935) and Sprague (1946) suggested that evaluation of lines at the $S_0$, $S_1$, or $S_2$ generation would identify lines with above average combining ability and, consequently, that selection among and within lines in future generations would include only lines having above average combining ability. Richey (1945), Singleton and Nelson (1945), and Payne and Hayes (1949) did not support the value of early testing, believing further selection among and within lines during each generation of inbreeding would be more effective use of resources. The highly inbred, elite group would be evaluated in testcrosses for their relative combining ability. The compromise in use of resources to evaluate lines in earlier generation ( $S_0$, $S_1$, $S_2$) of inbreeding versus evaluation of a smaller number of highly selected more inbred lines ( $S_5$, $S_6$, $S_7$) depends on the effectiveness of visual selection during inbreeding. Generally, the associations between traits of inbred lines and the same traits in their hybrids have been poor and of limited predictive value (Hallauer and Miranda, 1988).

Hallauer and Lopez-Perez (1979) evaluated combining abilities of 50 $S_1$ and 50 $S_8$ lines developed by single-seed descent, without selection, from BSSS in testcrosses with five testers. Average genetic correlations for all testers between $S_1$ and $S_8$ testcrosses for grain yield was $r_g$ = 0.34, ranging from $r_g$ = 0.17 to $r_g$ = 0.56. Jensen et al (1983) practiced selection among and within lines developed from elite germplasm until the $S_5$ generation of inbreeding. $S_1$ and $S_5$ testcrosses using B73 and NSS testers were evaluated for grain yield: average phenotypic correlations between $S_1$ and $S_5$ testcrosses were $r_p$ = 0.61 (B73) and $r_p$ = 0.73 (NSS). Hallauer and Lopez-Perez (1979) and Jensen et al. (1983) also compared yield of lines themselves with their respective testcross yields. The early-generation testcross yields were better predictors of later-generation testcross yields than were the lines themselves because average correlations between line performance and their crosses were $r_p$ = 0.14 (Jensen et al., 1983) and $r_g$ = 0.04 (Hallauer and Lopez-Perez, 1979). The correlations reported by Hallauer and Lopez-Perez (1979) and Jensen et al. (1983) are consistent with reports (Hallauer and Miranda, 1988) that inbred traits have limited relation to their hybrid traits.

The genetic correlations for yield between the $S_2$ and later generation testcrosses of BS13(S2)C1 ($r_g$ = 0.97) and BSCB1(R)C7 ($r_g$ = 0.86) support the original intent of early testing; i.e., combining ability of inbred lines in topcrosses is established relatively early during the inbreeding process and remains relatively stable with further inbreeding (Jenkins, 1935). Although intense selection was practiced during inbreeding after the $S_2$ generation in the development of the lines (Table 1), selection did not affect the mean performance of the lines in $S_2$ and later generation testcrosses (Table 2). Visual selection for plant and ear traits and pest resistance of the inbred lines themselves did not affect the average combining ability of the two groups of lines. There was some suggestion, but not convincing, of greater variation among the later generation testcrosses than among the $S_2$ testcrosses for percentage of root lodging and ear height, but there was no suggestion of differences in variability among $S_2$ and later generation testcrosses for the other traits (Table 3).

Our results support the concept of early testing to evaluate combining ability of newly developed lines (Table 4). The genetic correlations exceeded $r_g$ = 0.6 for grain yield and moisture, root lodging, days to anthesis, and ear height. Selection for desirable plant and ear traits and pest resistance can be continued during the inbreeding process, and continued selection will not have a significant affect on testcross performance (i.e., combining ability). The ultimate value of newly developed lines is their performance in hybrids. The cumulative evidence is clear that early testing will identify lines that have above average combining ability. Further selection is emphasized among and within lines having above average combining ability and greater potential as parents of hybrids. It seems the intense selection during inbreeding was effective to improve combining ability in comparison with lines developed by single-seed descent with no intentional selection (Hallauer and Lopez-Perez, 1979). Selection within and among lines during inbreeding obviously was not detrimental to their hybrid performance in the different generations. Mean performance was similar

for the $S_2$ and later generation testcrosses, but performance between generations of selected lines was more consistent than for unselected lines.

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